

California Press. ISBN 9780520255913. 508 p. \$95.00 (hardcover).—The iguanian lizard genus *Anolis* was once divided into several subgenera (Savage and Guyer, 1989), most of which proved not to be monophyletic. The present book stresses the phenomenal species richness of this apparently monophyletic clade of arboreal lizards (Nicholson et al., 2005), which by Losos's count consists of about 361 currently recognized species (others will doubtlessly be described). (As of 22 February 2012, The Reptile Database [<http://www.reptile-database.org/>] listed 391 valid species.) Although several subgenera (*Chamaeleolis*, *Chamaelinorops*, *Norops*) appear to be monophyletic, Losos chooses to place all in a single genus, *Anolis*, using subgeneric names between generic and specific names where necessary. Anoles have undergone a massive adaptive radiation in the West Indies, where many island endemics occur, and in Central and South America. A few are bizarre: one heavy bodied slow-moving Cuban species (*A. [Chamaeleolis] chamaeleonides*) plus a few close relatives has converged on the chameleon phenotype, and another species from Ecuador (*A. proboscis*) sports an elongate proboscis on its snout. This book is an instructive compendium of everything you always wanted to know about anoles, but were afraid to ask.

The late Ernest Williams and his students, especially Stan Rand and Tom Schoener, pioneered studies of Caribbean anoles (Rhodin and Miyata, 1983). Rand (1964) developed the useful concept of the structural niche: a combination of perch diameter and perch height. Williams (1983:326) invented and championed the idea of ecomorphs, defined as "a set of animals showing correlations among morphology, ecology, and behavior, but not lineage." Noting that ecomorphs had evolved independently on different islands in the Greater Antilles, Williams identified six ecomorphs among anoles. Grass-bush anole species are small and slender, occurring close to the ground on narrow perches, whereas trunk-ground species are heavier bodied and medium-sized using tree trunks as perches from which they forage on the ground. Trunk species are also medium in size but are typically found higher up on tree trunks. Twig species are very small and slender, occurring well above ground where they seldom leave narrow perches. Trunk-crown species are large and are found high up on tree trunks and in the low canopy. As their name implies, crown giants are huge and dwell in the tops of trees. All of these ecomorphs occur repeatedly among different islands in the Greater Antilles, but some are missing from some islands. Williams (1983) also recognized sun- and shade-seeking anole species. Sun species actively thermoregulate by basking, whereas shade species are passive thermoconformers with body temperatures close to ambient air temperatures (Huey, 1974). The latter species are threatened by global warming (Huey et al., 2009).

Anoles are typical iguanian lizards in many ways. Most are gray, brown, or green (*A. gorgonae* is bright blue!), and they can change color. Most have a uniform color pattern but some are blotched or striped. Females are often drab compared to males. Like most other iguanians, most anoles are small- to medium-sized ambush predators, hunting visually from perches, and they are largely insectivorous with relatively generalized diets (a few eat snails). Body size, relative limb length, and tail length are quite variable among species.

However, anoles differ from most other iguanians in several ways: they have a fixed clutch size of one, most have a prominent extensible dewlap, and they sport sticky subdigital toepads that greatly facilitate climbing. The fixed

clutch size of one in anoles has been suggested to be a mass-reduction adaptation that facilitates climbing (Andrews and Rand, 1974); nevertheless, female anoles compensate by pumping out eggs contralaterally at a high rate. Dewlaps vary in size and color and are used in social displays and species recognition. Losos identifies their adhesive toe lamellae as the primary "key innovation" that allowed diversification of anoles. Adhesive toe lamellae have evolved independently at least three times among lizards: in anoles, geckos (probably several times), and a small group of arboreal New Guinean skinks (*Lipinia leptosoma* and three species of *Prasinohaema*). Toe pads of gekkonine geckos have many more subdigital lamellae than anoles, which likely make geckos better climbers than anoles. Geckos as a group are species rich with more than 1200 species: one clade, the *Phelsuma* day geckos, has undergone a conspicuous adaptive radiation. Found primarily on Madagascar, Mauritius, and other islands in the Indian Ocean, *Phelsuma* are arboreal, diurnal, mostly green lizards that exhibit some similarities to anole assemblages (Harmon et al., 2007).

Anoles have many predators, especially birds, but also snakes and other lizards, even other larger anoles. They rely largely on cryptic coloration to escape notice: when a potential predator is nearby, they hug their perch and slowly rotate around and away to get out of view. They can also jump and change perches. If really threatened, some launch themselves off their perch and fall to the ground. Others run across streams, their bodies supported by the surface tension of the water.

While an undergraduate at Harvard, working with Williams and his last graduate student Greg Mayer, Losos completed his honors thesis on social behaviors of *Anolis*. During graduate school at the University of California, Berkeley, sponsored by Harry Greene, Losos explored possible dissertation projects on several other lizard groups (monitors, geckos, and chameleons) before succumbing to his destiny and returning to anoles. (I recall receiving a message from Losos as he was heading to Australia announcing, "I am going to do what you should have done, and watch *Ctenotus* skinks." I responded advising him that *Ctenotus* were much too cryptic to watch. He returned with some observations on the most abundant and conspicuous agamid *Ctenophorus isolepis* [Losos, 1987], but never published on *Ctenotus* skinks.)

The first chapter of *Lizards in an Evolutionary Tree* likens studying evolutionary biology to a detective's investigation, trying to elucidate what happened in the past from elusive information available in the present day. History is singular but exceedingly difficult to reconstruct. Essentially, a phylogenetic framework offers evolutionary biologists a sort of time machine (provided the phylogeny is accurate) with which probable ancestral traits can be inferred from those of extant species (e.g., Huey and Bennett, 1987). True phylogenies are almost never known and estimated trees are hypotheses that may not always be accurate. If ancestral states can be correctly postulated, the polarity of trait changes can be reconstructed. Stressing that reconstruction of ancestral traits may not be reliable for traits that evolve rapidly, Losos exploits phylogenetic trees (hence the play on words in the book's title) in multiple such attempts to ascertain the probable course of past evolutionary events.

Chapter 2 reviews anole biology, with descriptions and discussion of dewlaps, toepads, eyes, reproduction, head-bobbing and dewlap displays, reproductive isolation, phylogenetics, and geographic distribution and diversity.

Using cluster analysis and multivariate principal components, Chapter 3 is devoted to a detailed discussion of anole ecomorphs in the Greater Antilles (Cuba, Jamaica, Hispa-

niola, and Puerto Rico plus some nearby smaller outlying islands). Losos critically evaluates ecomorphs and concludes that Williams's choice of six is correct. Losos argues that they provide an exceptionally powerful and unique system for the study of evolution, especially with regard to replicated adaptive radiations (i.e., Williams's ecomorphs). The separation of ecomorphs on body size, structural niches, and height above the ground is a great example of resource partitioning that should reduce competition between species. Sun- versus shade-anole species have diverged along a different niche dimension: microclimate. Prey sizes differ among sympatric anole species on Bimini (Schoener, 1968), potentially reducing interspecific competition. Chapter 3 concludes with an interesting appendix on the history of studies on ecological morphology in anoles.

Chapter 4 describes unique non-ecomorph anoles from the Greater Antilles as well as those occurring on smaller land-bridge and oceanic islands, including the Bahamas. The species-area relationship of West Indian anoles and faunal relaxation are briefly discussed. Successful colonization appears to have been infrequent. The Lesser Antilles are the chain of small islands stretching from east of Puerto Rico to Grenada just north of South America—each of these small islands supports only one or two anoles, which do not fall neatly into ecomorph categories and typically exhibit intra-specific geographic variation. If an island has two species, one is large and the other small. Such size differences between sympatric anole pairs in the Lesser Antilles could be examples of character displacement to reduce or avoid interspecific competition. This chapter concludes with a brief description of little known “mainland” anoles in central and South America, where anoles are generally far less abundant (and much less well studied) than they are on Caribbean islands. Several of these mainland anoles are aquatic.

Chapters 5 and 6 are devoted to phylogenetic inference, describing methods of plotting traits on trees and inferring probable ancestral states. Anole phylogeny and taxonomy are briefly discussed. The biogeography, probable dispersal events, and origin of anoles are also covered. In the next chapter, the probable sequences of evolution of ecomorphs on Jamaica and Puerto Rico are once again reconstructed using these methods. Some ecomorphs are perplexingly missing from some islands. A principal component analysis clearly separates ecomorphs.

Anole life history and population biology are described in detail in Chapter 8 (“Cradle to Grave”), including reproduction, growth, dispersal, survival, predators, parasites, population density and fluctuations, foraging mode, and diets. Usually, anoles appear to be food limited, but predation pressures are probably heightened in mainland habitats where they could be important. A detailed analysis of sexual dimorphism, sexual selection, and social behavior ensues. Most species of anoles are sexually dimorphic, with larger males defending territories occupied by usually smaller females and juveniles. Large males can defend larger territories and thus have access to more females. Larger males copulate more frequently than smaller males. Females do not appear to exhibit much evidence of mate choice, but further studies are needed. The degree of sexual dimorphisms in size and shape varies among ecomorphs with twig species showing the least dimorphism and trunk-crown and trunk-ground species being most dimorphic (crown giants are not exceptionally dimorphic in size, but do show extreme dimorphism in shape).

Habitat use and thermoregulation are reviewed next. Ecomorphs differ little in active body temperatures. Island anoles have higher body temperatures when active than

most mainland species, which tend to occur in shadier microhabitats. Most anoles sleep on leaves or the ends of branches higher up and on narrower perches than those used during the day, probably as a means of avoiding predators—if a predator causes the branch to vibrate, anoles can jump off to evade predators. Some snakes catch anoles at night by approaching from an unconnected branch.

Anoles partition resources along three primary niche dimensions: structural microhabitat, thermal microhabitat, or prey size. Some mainland anoles also separate out along a habitat dimension. Species or size/sex classes similar along one niche dimension usually differ along another dimension. Such complementarity of niche dimensions (Schoener, 1968) presumably reduces competition, facilitating coexistence. Removal and introduction experiments and subsequent niche shifts, especially in habitats and microhabitats, strongly support this interpretation.

Following statistical removal of the effects of body size, relative leg length across species of *Anolis* is correlated with perch diameter. Moreover, at least one species exhibits developmental plasticity: *A. sagrei* raised in cages with broad surfaces grew relatively longer hind legs than those raised in cages with narrow perches. Lengths of forelimbs, hind limbs, and tails correlate positively with sprint speed, jump distance, and clinging ability. Long legged species are more prone to jump and run, whereas short-legged species walk more frequently.

Adaptive radiations of other organisms such as Galápagos finches, African rift lake cichlid fishes, *Phelsuma* geckos, Japanese *Mandarina* snails, and Hawaiian *Tetragnatha* spiders, are briefly considered. Strangely, in all probability the second-largest adaptive radiation among lizards, Australian skinks of the genus *Ctenotus* with about 100 currently recognized species (Rabosky et al., 2007), is not mentioned.

The book concludes with brief discussions of conservation biology, climate change, habitat destruction, invasive anoles, and the uncertain future facing these interesting lizards. The International Union for the Conservation of Nature lists 23 species of *Anolis* as threatened: two are critically endangered, 14 endangered, and seven are vulnerable (IUCN, 2011.2).

Bravely, Losos does not shy away from speculation, opening himself up for criticism by telling “adaptationist stories” (Gould and Lewontin, 1979:581). Indeed, he uses concepts like “historical contingency,” “ecological opportunity,” “empty niches,” “disparity,” and “evolutionary constraints” freely, and coins new words for concepts as elusive as “modularity,” and “evolability.” Losos identifies numerous directions for fruitful future research on anoles, inviting others to join in their study. This thoughtful and informative book is written in a very friendly conversational style with hundreds of footnotes. Every lizard ecologist will want to read it.

As usual, the University of California Press has done a splendid job on this book, which won the Daniel Giraud Elliot Medal. However, their copy editors overlooked a minor error in the references section: a citation to their own coffee table book *Lizards: Windows to the Evolution of Diversity*, coauthored by myself and L. J. Vitt has the order of authorship reversed!

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major areas of cytogenetic and genomic evolution research, with contributions on Genome Composition, Molecular Evolution and Phylogeny, Chromosomal Evolution and Phylogeny, Chromosome and Genetic Mapping, Sex Chromosomes, Parthenogenesis, and Chromosome Dynamics. As each section is written by different investigators, the tone varies from chapter to chapter, but the overall presentation is clear and readable. Accordingly, the techniques covered range from cutting-edge sequencing to more traditional methods such as FISH and immunofluorescence staining, and the scope of the material ranges from genome evolution across squamates to detailed genome mapping of single species (e.g., *Crocodylus porosus*, *Sphenodon punctatus*). There is thus a mixture of process-based evolutionary analyses and pattern-based descriptions of cytogenetic and genomic arrangements, though both have their place in an overview such as this. Highlights include Castoe et al.'s review of mitochondrial genome evolution in squamates, Hall's overview of chromosome evolution in *Sceloporus*, O'Meally et al.'s cytogenetic map of the tuatara (*S. punctatus*), and Fujita and Moritz's overview of parthenogenesis in lizards. There are also data on an interesting system of tissue ploidy diversity, with both diploidy and triploidy within individuals and among members in some Surinam populations of the turtle *Platemys* (Bickham and Hanks).

The primary question when dealing with a review volume in such a rapidly changing field as genomics is not how timely the data are, as many of the articles will inevitably be out of date as soon as they are printed, but how well the contributions capture the current state of the field, as well as future directions. Indeed, early chapters lament the paucity of genomic sequence data, as only the genome of *Anolis* and draft of the genome of *Chrysemys* had been completed by that point, while there is now at least one snake genome (Castoe et al., 2011). In addition, many phylogenetic hypotheses upon which comparative analyses are based are outmoded given recent developments in molecular systematics. The final chapter even uses the genus name *Natrix* for species now placed in *Xenochrophis*. However, overall the contributions give an expansive view of the state of cytogenetics and genome evolution, which is no small feat considering the breadth of material covered. There are in-depth reviews of evolution in structure and function of both nuclear and mitochondrial genomes in squamates, as well as sex-determination mechanisms, the origins of parthenogenesis, and the evolution of sex chromosomes. Detailed genetic maps and chromosome ideograms are given for archosaurs and rhychocephalians. Many of these chapters will be invaluable starting points for anyone interested in studying genomics, and because these are contributed papers, the literature cited with each contribution is extensive and varied.

As our knowledge of the reptilian genome and cytogenetic variation increases, many of the questions posed by this book will be answered, some of the hypotheses corroborated, and likely some conjectures disproven. However, as a summary of the field, the book succeeds. The development of phylogenomics in both senses (i.e., using genomes to infer phylogenetic histories and phylogenies to infer genome histories) will require increased amounts of data on species-level cytogenetic and genomic attributes to harness the power of those data for reconstructing evolutionary histories. Karyotypes, for instance, have only been produced for approximately 1000 of the >9300 reptile species. Similarly, data on sex-determination mechanisms is lacking from many groups. The need for these data is made clear in the volume, which sets a strong foundation for

**Reptilian Cytogenetics and Genomics.** E. Olmo (ed.). 2010. Karger Press, ISBN 9783805594905. 226 p. \$164.00 (hardcover).—Genomics is a field in constant flux, as new technologies for genome sequencing and techniques for cytogenetics offer increasingly detailed views of the genome. This book, an edited volume consisting of a 2009 special issue of *Cytogenetic and Genome Research* (Vol. 127, No. 2–4), is an attempt to give an overview of the state of our knowledge of cytogenetics and genome evolution in reptiles (in the traditional sense of squamates, archosaurs, and chelonians). The book is divided into sections covering